

# TIDAL RHYTHMICITY OF RATE OF WATER PROPULSION IN MYTILUS, AND ITS MODIFIABILITY BY TRANSPLANTATION <sup>1, 2</sup>

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While studying the rate of water propulsion in *Mytilus californianus* (Rao, 1953) it was observed that the behavior of the mussels was not the same at different periods of the day. A detailed study revealed that these differences were of the nature of a tidal rhythm, with periods of greater activity, corresponding to the times of high tide, alternating with those of lesser activity, corresponding to the times of low tide in the area from which the animals were collected.

Since the discovery of a persistent tidal rhythm in *Convoluta roscoffensis* (Bohn, 1903; Gamble and Keeble, 1903), similar rhythms have been described for a number of marine organisms from nearly all groups, and these have been reviewed by Calhoun (1944) and Brown, Fingerman, Sandeen and Webb (1953). Several molluscs have been described as exhibiting tidal rhythmicity in their activity. *Littorina rudis*, which is covered by water only during the semilunar high, high tides, becomes active at 15-day intervals when kept in the laboratory (Bohn, 1904). Brown, Bennett and Graves (1953) report a long-term tidal rhythm in *Venus*. Gompel (1937, 1938) reported the occurrence of a persisting tidal rhythm of oxygen consumption in *Patella*, *Mytilus*, *Pecten* and *Cytherea* while in *Halotis tuberculata* it was not so marked. Brown, Bennett and Webb (1953) found the same in the crab *Uca*.

In the following studies an attempt was made to learn something of the nature of this rhythm in *Mytilus*, using as an index of activity the rate of water propulsion.

It is a pleasure to acknowledge my indebtedness to Professor Theodore H. Bullock for helping me in the procurement of the material; offering me all the laboratory facilities; for his enthusiastic encouragement during the course of this investigation and for critically reading through this paper. To the Chairman and Secretary of the Department of Zoology, and the other members of the staff, I am most grateful for several courtesies extended to me during my stay in the Department. My especial thanks are due to Professor G. E. MacGinitie, Director of the Kerckhoff Marine Laboratory, Corona del Mar, California, and to his staff for allowing me to make use of their laboratory pier for the experiment in transplantation of mussels. Finally I should like to place on record the promptness with

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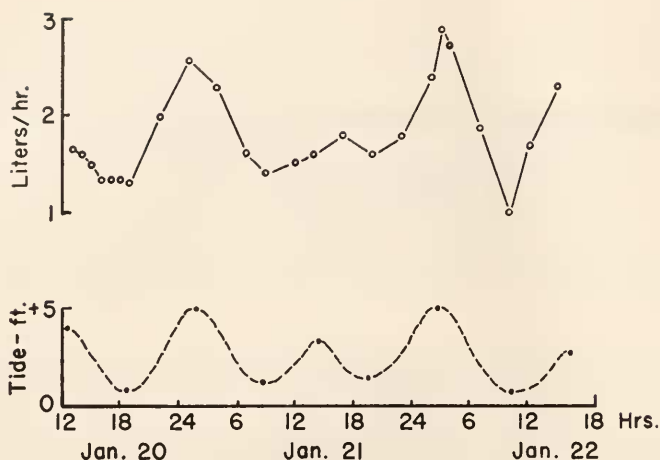


FIGURE 1. Variations in the rate of water propulsion in a single specimen of *M. californianus* collected inter-tidally from +1.0 ft. and kept in darkness at  $14 \pm 1^\circ$  C. Dotted line indicates the tidal cycle in the locality of collection, in this and the following figures.

which the Supply Department of the Marine Biological Laboratory, Woods Hole, Massachusetts, sent us the required supply of *Mytilus edulis*.

#### MATERIALS AND METHODS

*Mytilus californianus* collected from about +1.0 ft. (tidal datum zero is mean lower low water, tidal range here about 8 feet) on pilings at Santa Monica, California, were transferred to aquaria containing sea water at  $14 \pm 1^\circ$  C. One large mussel was placed in each of three enamel-coated pans containing sea water at  $9 \pm 1^\circ$ ,  $14 \pm 1^\circ$ , and  $20 \pm 1^\circ$  C., respectively, while a duplicate series of three pans contained ten to twelve mussels each, at the same three temperatures. All

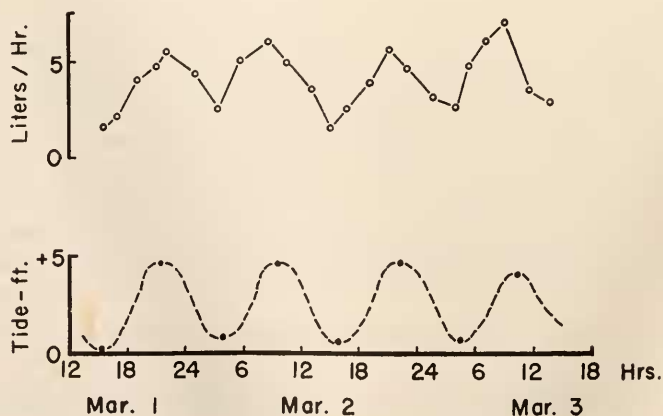


FIGURE 2. Rhythmicity in the rate of water propulsion in *M. californianus* collected from a depth of about 30 ft. off Los Angeles, and kept in darkness at  $14^\circ$  C.

the containers were covered with lids, making them virtually dark chambers. The method used for measuring the rate of water propulsion has been detailed elsewhere (Rao, 1953). Measurements were made at hourly intervals round the clock for 72 hours in continuity and this was repeated at three-day intervals, over a period of four to six weeks.

The same procedure as above was followed for *M. californianus* from about + 4.0 ft., on pilings and for *M. edulis* from pilings and from the underside of floats a few feet away. A collection of *M. californianus* obtained from a depth of about 30 ft. off the shore near Los Angeles, and a consignment of *M. edulis* collected at

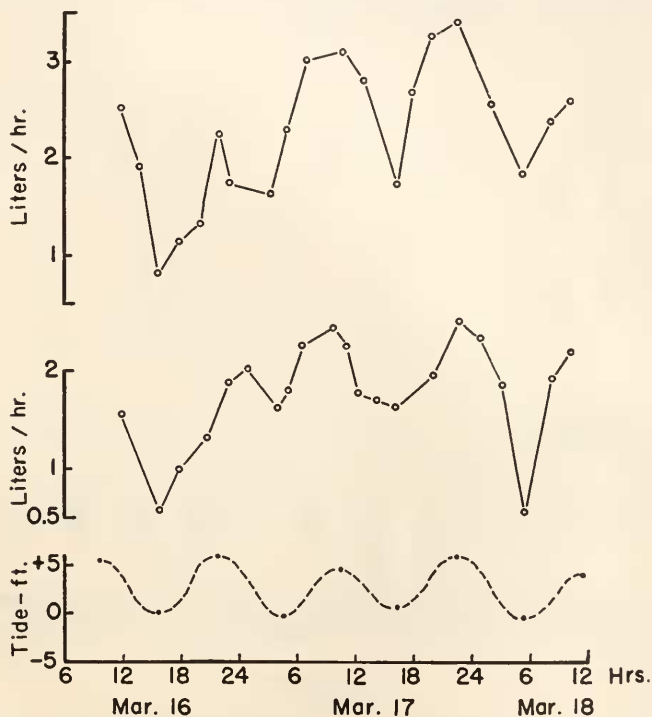


FIGURE 3. Variations in the rate of water propulsion over a period of 48 hours in *M. edulis* collected from floats and pilings at Santa Monica, California, and kept in darkness at  $14^{\circ}\text{C}$ . Upper graph for animals from floats and the lower one for those from pilings.

Barnstable Harbor on Cape Cod and flown to Los Angeles, California, were studied at  $9 \pm 1^{\circ}\text{C}$ . and  $14 \pm 1^{\circ}\text{C}$ .

Besides measurements on animals kept in continuous darkness, all the above samples were subjected to continuous light and the natural day and night environment and measurements made.

## RESULTS

### *Mytilus californianus*

Individuals of *M. californianus*, when observed in the laboratory, exhibit a pattern of activity (measured by the rate of water propulsion) which corresponds in

time and degree to the tidal levels in the locality from where they have been collected (Fig. 1). The pattern holds good even when several individuals are grouped together and their activity as a whole is measured. The rhythm is independent of temperature over the whole range measured, from 9 to 20° C. (as has been found by Brown, Bennett and Sandeen, 1953, in the fiddler crab) and persists for over four weeks in the laboratory in continuous darkness or continuous light, or the normal day and night environment. No indications of a diurnal rhythm in the rate of water propulsion were noticed.

Similar results were obtained regardless of the height inter-tidally from which animals were collected and even with mussels obtained from a sub-tidal population at a depth of about 30 ft. off the shore (Fig. 2).

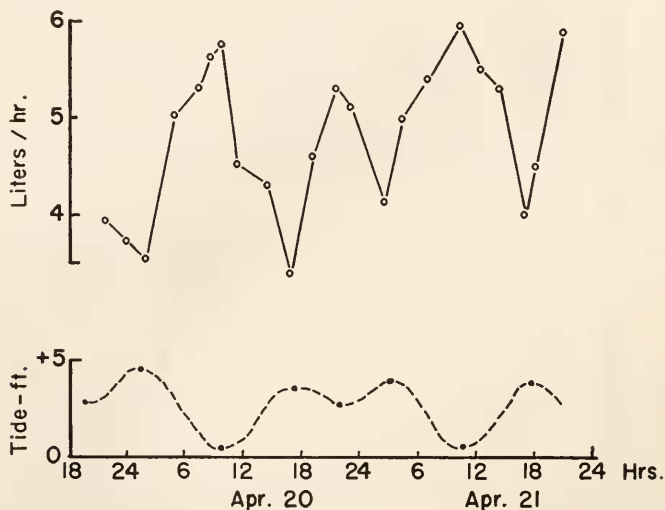


FIGURE 4. Record of rate of water propulsion in *M. edulis* from Barnstable Harbor on Cape Cod, kept in darkness at 9° C. at Los Angeles, California. Dotted line indicates the tidal cycle at Los Angeles.

### *Mytilus edulis*

Samples of *M. edulis* collected from the same locality and treated similarly showed a tidal rhythmicity in their rate of water propulsion. What is more remarkable, mussels collected from the underside of floats showed a pattern of activity which was quite parallel to that exhibited by mussels collected from the pilings nearby (Fig. 3).

*M. edulis* collected at Barnstable Harbor on Cape Cod and studied at Los Angeles, California—nearly 3000 miles west—showed a rhythm in their rate of water propulsion which was out of phase with the local tidal cycle by about 6½ hrs. (Fig. 4), and this difference persisted for over four weeks in the laboratory.

Of the mussels obtained from Cape Cod, one dozen were kept in a small wire cage and, during low tide, were secured at +1.0 ft. to a piling of the pier at the Kerckhoff Marine Laboratory, Corona del Mar, California, to study the effect of the local tidal schedule on these mussels. After a week's sojourn at this place,

they were brought back to the laboratory along with a sample of local *M. edulis* attached to the same piling at the same inter-tidal height, which served as controls for the experimental animals. Study of the activity pattern (at 9 and 14° C.) revealed a prompt shift in the rhythm to synchronize with the local tidal cycle and

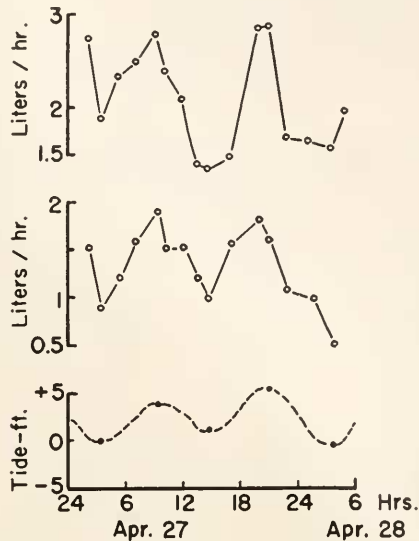


FIGURE 5. Record of rate of water propulsion in *M. edulis* from Barnstable Harbor on Cape Cod, after having been kept for one week at +1.0 ft. in the inter-tidal at Corona del Mar, California, and of the control. Upper graph for *M. edulis* transplanted from Barnstable Harbor, and lower graph for mussels from pilings at Corona del Mar, California, serving as control. Dotted line indicates the local tidal cycle.

there is found to be good agreement between the transplanted east-coast mussels and the local controls (Fig. 5). They continued to keep in phase with the local tidal cycle for a period of over three weeks in the laboratory.

#### DISCUSSION

A marked tidal rhythmicity of rate of water propulsion is exhibited by populations of *Mytilus* occurring under a great variety of environmental conditions and persists in the laboratory for long periods (over four weeks) in phase with the tidal cycle of their natural environment, independent of a wide range of temperature (9 to 20° C.) and varying conditions of light and darkness. That it exhibits the same frequency in populations from high and low inter-tidal levels and even in sub-tidal populations (30 ft. deep) and that it persists in the laboratory, in phase with the tidal cycle outside, for long periods under constant conditions, demonstrate the intrinsic (or endogenous) nature of the rhythm.

It is most interesting that such a rhythm is evident in populations from the underside of floats (and hence not subject to the direct physical effects of the tides), with the same frequency and in phase with the local tidal cycle. It is equally of interest that a persistent rhythm with the same frequency, but out of phase with



the local tidal cycle, is exhibited by mussels removed nearly 3000 miles west from their natural environment. Such instances as these indicate that the rhythm, once set, is independent of external factors, such as cosmic influences, and can persist over long periods in the laboratory.

Instances like the foregoing demonstration of a tidal rhythm in a single species under a great variety of natural conditions lead one to suppose that organisms in general have rhythmic properties and that the frequency of the rhythm is intrinsic and perhaps inherited. But how such intrinsic rhythms at a given frequency come to be in synchrony with rhythmic events in nature is difficult to answer. But the ease with which they can be reset to suit a new environment, without a change in the frequency, though not abundantly demonstrated, is of sufficient significance inasmuch as it helps us to understand the existence of so many instances of tidal or other kinds of rhythmic behavior patterns. An intrinsic, inherited rhythmic pattern of activity is set in phase with external events of a rhythmic nature, which perhaps are of the same frequency as the organismic ones. Transplantation, as has been done for the first time in the above case, offers an ideal tool for studying this phenomenon in greater detail. Likewise, studying laboratory-grown individuals of species which show a rhythmic behavior in their natural environment, might yield fruitful results.

But the degree to which the rhythm is marked, perhaps, is dependent on the amplitude of the environmental rhythm. Thus the different findings (Bohn and Piéron, 1906; Bohn, 1906, 1907; Piéron, 1906, 1908; Gee, 1913; Parker, 1916; Crozier, 1921, and Hoffman, 1926) on the rhythmic behavior in sea anemones may be due to the fact that the intrinsic rhythm becomes marked and measurable only when the fluctuations of the environmental factors reach a certain, but unknown, threshold value.

#### SUMMARY

1. The occurrence of a tidal rhythm in the rate of water propulsion in *Mytilus californianus*, collected from high and low inter-tidal levels and from a depth of 30 ft. off the shore, and also in *M. edulis* collected from pilings and the underside of floats, has been demonstrated.

2. Such a rhythm is independent of temperature (9 to 20° C.) and persists in the laboratory, in phase with the external tidal cycle, for over four weeks, in continuous darkness, or continuous light or the natural day and night environment.

3. No indications of a diurnal rhythm in the rate of water propulsion have been observed.

4. A rhythm of similar frequency, but out of phase with local tidal cycle by about 6½ hrs., was observed in *M. edulis* collected from Barnstable Harbor on Cape Cod and studied at Los Angeles, California, after transporting them by air.

5. Some of the east coast mussels were secured in the inter-tidal at Corona del Mar, California, for a week. Examination of their activity pattern after this period, revealed a prompt shift in their tidal rhythm to synchronize with the local tidal schedule.

6. The intrinsic nature of the rhythm is discussed and the probable inheritable nature of the rhythmic properties of organisms, coupled with the ease with which they could be set in synchrony with natural environmental rhythms, are suggested as likely causes for the widespread occurrence of rhythmic patterns in organisms.

7. It is suggested that the degree to which the intrinsic rhythm of the organism becomes marked and measurable depends upon the amplitude of the environmental rhythm.

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